Attention focusing in a sit-and-wait forager: a spider controls its prey-detection ability in different web sectors by adjusting thread tension

Kensuke Nakata*

Department of Contemporary Law, Tokyo Keizai University, Minami-machi 1-7-34, Kokubunji, Tokyo 185-8502, Japan

Focusing attention is a way for animals to search for and to obtain food efficiently. This study examines whether a sit-and-wait forager, the orb-web spider *Cyclosa octotuberculata*, focuses its attention on limited foraging areas. Video records of foraging activity revealed that the spiders detected prey trapped in the west and east sectors of their web less frequently than prey trapped in the north and south sectors. Comparison of photos of the web hub area with and without spiders present revealed that the spiders pulled radii towards the centre when waiting for prey. Radius pulling is stronger in the north and south web sectors than in the west and east sectors, possibly causing more tension in radii running vertically. Experimental manipulation indicated that the spiders responded to prey quicker when thread tension was increased. The results suggest that *C. octotuberculata* focus their attention on the web areas above and below the spider by adjusting the tension in web threads; and this causes higher prey detection rates in these areas.

Keywords: spider; attention; orb web; foraging; sense

1. INTRODUCTION

Foraging animals often direct their search activities towards pre-determined targets or areas which become the focus of their attention. Foragers using search image limit their search to particular targets within an array of various potential food items (Langley 1996), whereas other foragers spatially concentrate their search efforts on a limited area, a phenomenon referred to as area-restricted search (Fauchald & Tveraa 2003). These strategies allow animals to discard or filter out excess sensory information that could overwhelm their cognitive resources, and can raise prey detection rates and enhance foraging efficiency (Dukas & Kamil 2001).

Foraging animals encounter food in two ways: widely foraging animals actively move around to search for food, whereas sit-and-wait foraging animals are motionless and capture food that comes sufficiently close (Schoener 1971). Attention focusing in animals has been studied mainly in widely foraging vertebrates such as birds (Dukas 2002), and attention focusing in sit-and-wait foragers warrants further study. Attention focusing may have benefits for sit-and-wait foragers, but because of their passive nature they may also suffer by limiting their food-acquiring opportunities. The 'syndrome hypothesis' suggests that widely foraging and sit-and-wait foraging animals are different not only in patterns of movement when foraging, but also in other ecological and physiological characteristics (McLaughlin 1989).

Orb-web spiders are sit-and-wait invertebrate foragers in terrestrial ecosystems. They typically wait for prey

while sitting at the web hub, the central part of the web where the radii converge. Predation behaviour starts when the spider becomes aware of intercepted prey trapped in the web, and tries to locate it by plucking radii (Díaz-Fleischer 2005). When the prey is detected the spider moves to it and capture follows if the web retains the prey long enough; but the prey sometimes escapes before the spider reaches them (Zschokke *et al.* 2006).

Do orb-web spiders focus their attention on limited web areas when waiting for prey? If they did, they would detect prey trapped in specific web areas more efficiently. This study examines this possibility in the field population of the orb-web spider *Cyclosa octotuberculata*. This study also examines *C. octotuberculata*'s thread-tension-adjusting behaviour. Tactile senses are a web spider's primary sensory modality (Barth 2002). They place their legs, which possess hair sensillae, on radii through which vibrations from prey trapped in the web are transmitted (Barth 2002). Thus, an orb web functions as a tactile sensory structure that extends beyond the spider's body. The transmission efficiency of web-borne vibrations is affected by thread tension, and spiders may be able to control the sensitivity of a web by adjusting the tension of radii (Watanabe 1999). Initial observations showed that *C. octotuberculata* pulls on radii when waiting on the web hub for prey (figure 1). The effect of radius-pulling behaviour on web contraction towards the hub was examined to determine whether radial contraction was stronger in specific areas of the web. The effect of increases in thread tension on prey-detection efficiency was examined. The directional tendencies of prey-detection rates and thread-pulling behaviour were also examined to determine if the spiders focus their attention on particular web sectors.

*ken@tku.ac.jp

Figure 1. Central area of an orb web of *C. octotuberculata*. The picture was made by superimposing a photo of the web with the spider pulling on radii (the threads are highlighted in white) on a photo of the web without the spider present (the threads are highlighted in red). Debris decorations in the photo of the web without the spider were clipped out so as not to obscure the spider in the superimposed image. See §2 for explanation of j_k and j'_k .

2. MATERIAL AND METHODS

Cyclosa octotuberculata is a diurnal spider that builds vertical orb webs with debris decorations that include prey remnants, its own moulted exoskeletons and egg sacs during the breeding season. The debris decorations are linearly arranged and attached to the web vertically through the hub (figure 1). A spider sitting on or within this debris is camouflaged and inconspicuous to the human eye. Normally, the spider builds its web at sunrise and knocks the web down the following night. On web rebuilding at the next sunrise, the debris decorations are re-used. From late April to May in 2003 and 2005–2008, 80 webs of adult or sub-adult females of *C. octotuberculata* were video-recorded at Mt. Inasa, Nagasaki City, Japan. Each web was observed for 80 min. The angular position relative to the hub of the web of each prey interception (0° vertical to 360° clockwise) was measured, and the fate of the prey was classified as follows. (i) Failure to detect prey, where the spider turned to the direction of the prey and plucked radii to locate it, but eventually stopped the locating behaviour and returned to a waiting posture. The prey remained on the web until the end of the observation. (ii) Successful capture of prey. (iii) Prey escape, where, during the locating behaviour or after the spider started moving to the located prey, the prey escaped before being captured. The angular distributions of each category were tested for uniformity versus significant mean angular direction by the Rayleigh test. The data were also doubled and a Rayleigh test was conducted to examine whether angular distributions had diametrical bimodality (Zar 1998). Orb webs are not perfect circles and the lower half of the web is larger than the upper half (see §3). Thus the angular distribution of prey interception is expected to be biased towards the south sector. Nevertheless, if the spider focuses its attention in specific directions, prey detection

would be more successful in those directions, and it would be expected that angular distributions of successful capture of prey events and failure to detect events would differ significantly. The Wheeler-Watson test (Zar 1998) was used to test this hypothesis. From the video image, prey size was also measured and classified into small (less than 5 mm), medium (greater than or equal to 5 and less than 10 mm) and large (greater than or equal to 10 mm) to examine the effect of prey size on the predation success and the angular distribution of trapped prey location on the web.

Adult female spiders and their debris decorations were collected in the field (16 spiders in 2005, 16 in 2006 and 18 in 2009). The spiders were acclimated to laboratory conditions with a natural day–night light regime for more than 5 days. Each spider was housed with its debris decorations in an individual transparent acrylic frame, where the spider built its webs with debris decorations. Temperature and humidity in the laboratory were not controlled. During this period, spiders that built webs were fed one syrphid fly a day. After acclimatization, radial-thread-pulling behaviour in the 32 spiders collected in 2005 and 2006 was observed and analysed for directional tendencies. Prior to each observation, the acrylic frame with the web inside it was placed on a photo stage similar to the one described in Zschokke & Herberstein (2005). The frame was left untouched for more than 15 min to remove the effects of handling: sometimes spiders contracted their legs in response to the disturbance from handling the frame, but these contractions did not persist for a long time. Each observation consisted of three photos. The first photo pictured the entire web with the spider sitting on the hub. The second photo pictured the hub and several innermost spiral turns, with the spider sitting on the hub and pulling on radii. After the second photo was taken, the spider was removed from the web without damaging the web, and the third photo was taken from the same camera position and with the same magnification. Distances were measured between the web centre and the junctions of an arbitrarily chosen spiral turn with each radius when the spider was present (j_k) and absent (j'_k ; figure 1), and the difference between them ($d_k = j'_k - j_k$) was calculated. The web plane was divided into four sectors: north (from 315° to 45° ; vertical was 0°), east (from 45° to 135°), south (from 135° to 225°) and west (from 225° to 315°). The maximum d_k in each sector was assumed to represent the strength of spider radius-pulling in each of the four directions. These values were averaged for horizontal (east–west) and vertical (north–south) directions. For each spider, the measurements were repeated two or three times in different webs built on different days. The total number of measurements was 87. An analysis of variance (ANOVA) with two repeated variables (measurement order and direction) was conducted to examine whether the average values of maximum d_k differed between vertical and horizontal directions. For the 16 spiders collected in 2005, the distance from the hub to the outermost spiral was measured at 20° intervals from 0 to 360° to illustrate the outline of the web shape.

The effect of increased thread tension on a spider's prey-detection efficiency was experimentally examined in the 18 spiders collected in 2009. In the experimental treatment, the tension of web threads was increased by pulling three or four anchor threads outwards and attaching the thread ends to the acrylic frame with adhesive tape. This increased the average horizontal diameter of the webs by 2.6 per cent, from 20.83 ± 4.84 cm (mean $\pm$ s.d.) to

21.38 ± 4.83 cm. Each spider's response time was then measured twice a day. In one measurement, a field-collected syrphid fly was used as large prey, and in the other, a fruit fly was used as small prey. In the measurement procedure, a small or large prey fly was picked up by its wing with fine forceps and gently placed on the web horizontal to the hub and 5 cm from it. When the subject spider became aware of the prey and started to turn to it, the fly was immediately removed to minimize the damage to the web owing to the spider running to the prey. The whole sequence was video-recorded and the spider's response time was measured as the time from the prey's contact with the web to the start of a spider's predatory behaviour, at a resolution of 1/30 s. The presentations of large and small prey were at least one hour apart and in different horizontal web sectors (i.e. west or east sectors). In nine of the spiders, measurements were first obtained on webs manipulated by pulling the anchor threads. When webs were rebuilt on the following or later day, they were used as non-manipulated controls. A spider's response times to large and small prey items were measured in the same way as with the manipulated webs. In the other nine spiders, the order of web treatment was reversed, i.e. observations were first obtained on control webs, and rebuilt webs were manipulated by pulling the anchor threads. Thus, a total of four measurements were obtained from each spider. The order of presentation of small and large prey items was randomly determined for each spider, but was consistent between measurements on the experimental and control webs for the same individual. Data were log-transformed and analysed using ANOVA with two repeated variables (web treatment and prey type) and one between-subject factor (the order of web treatment). The presentation order of small and large prey items was not used in the ANOVA, since preliminary analysis revealed that it had no effect on a spider's response time and inclusion of it made the analysis too complicated.

3. RESULTS

Among the 175 cases of total prey web-hits observed in the field, the spiders failed to locate small, medium and large size prey in 26, 5 and 0 cases, respectively. Spiders successfully captured the prey in 92 cases. The total captures were 69, 16 and 7 for small, medium and large prey, respectively. Prey size distribution did not differ between failures to detect prey and successful captures (2×3 Fisher exact probability test, $p = 0.367$). The prey escaped in the remaining 52 observed cases (24 small, 11 medium and 17 large prey). The fate of large prey was significantly different from that of small and medium-size prey (2×3 Fisher exact probability test, $p < 0.001$ and $p = 0.008$, respectively). The spiders detected all large prey hitting the web, but large prey escaped more frequently. No difference was detected between the fate of small and medium-size prey ($p = 0.264$).

The angular distribution of the failures to detect prey did not exhibit unimodality (mean angle = 259.1 , vector length = 0.181 , $p = 0.366$), but did exhibit diametrical bimodality (vector length = 0.470 , $p = 0.001$). Spiders often failed to detect prey trapped in the horizontal directions (figure 2a). The angular distribution of captures indicated that successful capture occurred more in the lower part of web than in the upper part (figure 2b;

mean angle = 185.5 , vector length = 0.258 , $p = 0.002$). The distribution of prey escapes did not show any directional tendency (figure 2c). There was a significant difference in the angular distribution of successful captures and the failures to detect prey (W value = 6.36 , d.f. = 2 , $p = 0.041$). This tendency held true when large prey, to which spiders might respond differently, were excluded from the analysis (W value = 6.27 , d.f. = 2 , $p = 0.043$). In figure 2, the web outline is also indicated as standardized average radius. The radius in the vertical down direction (13.43 ± 1.37 cm, mean $\pm$ s.d.) was longer than in the vertical up direction (17 ± 1.97 cm, mean $\pm$ s.d.), and the vertical diameter (30.43 ± 2.71 cm, mean $\pm$ s.d.) was longer than the horizontal diameter (28.80 ± 2.96 cm, mean $\pm$ s.d.); that is, *C. octotuberculata*'s web has up-down size asymmetry and is a vertically elliptic shape.

The examination of hub pictures revealed that spiders pulled radii more in the vertical direction than in the horizontal direction in 56 of 87 webs examined. Average values of maximum d_k were significantly larger in the vertical direction (3.11 ± 1.51 mm, mean $\pm$ s.d.) than in the horizontal direction (2.63 ± 1.30 mm, mean $\pm$ s.d., $F = 9.71$, d.f. = 1 , $p = 0.004$). Figure 3 shows the average response time of spiders to large and small prey on the control webs and the experimental webs in which thread tension was increased. Spiders responded more quickly to large prey than small prey, and to prey on the experimental web than the control web. Repeated ANOVA indicated that both of these factors (prey size and thread tension) were statistically significant (treatment: $F = 13.21$, d.f. = 1 , $p = 0.002$; prey size: $F = 5.17$, d.f. = 1 , $p = 0.037$). Interaction between them was not significant ($F = 0.19$, d.f. = 1 , $p = 0.666$).

4. DISCUSSION

Field observations revealed that the orb-web spider *C. octotuberculata* detected prey intercepted on web sectors on the spider's flanks less frequently than prey intercepted on web sectors above and below the spider. In the laboratory, the spiders were observed to pull on vertical radii more strongly than on horizontal radii. Orb-web spiders depend on mechanical senses to perceive events around them (Barth 2002), and events such as prey interception produce vibrations that are transmitted through the web threads and sensed by the spider (Masters & Markl 1981; Landolfi & Barth 1996). When the spider pulls on radii, the thread tension is likely to increase. Some studies suggest that webs are constructed with higher tension in the north sector and lower tension in the south sector (Wirth & Barth 1992; Köhler & Vollrath 1995). However, the actual tension of threads in *Cyclosa* webs has not been measured. If we assume that baseline tensions are the same in all threads, then pulling on the threads by the spiders should result in higher tension in vertical radii compared with horizontal radii. The efficiency of vibration transmission is thought to be enhanced when thread tension is increased. This hypothesis was supported by the quicker response of spiders to prey on the experimental webs in which thread tension was artificially increased. Similar experimental results have been reported in *Octonoba sybotides* (Watanabe 1999). This indicates that the directional

Figure 2. Rose diagrams indicating angular distributions for (a) failures to detect prey, (b) successful captures and (c) prey escapes. The black lines indicate the rates relative to total prey hits. Dotted lines indicate the average web shape. White triangles indicate the mean angle of raw data when the vector strength was found to be significant by Rayleigh test. Black triangles indicate the mean angle of doubled data when the vector strength was found to be significant by Rayleigh test. The vertical upward direction is 0°.

Figure 3. Average response time of spiders to small and large prey that were experimentally placed on control webs and on webs with increased thread tension. Vertical bars indicate s.e. Grey bar, control; white bar, tension increased.

differences in web radius-pulling behaviour make the owner spider less sensitive to prey impacts in horizontal web sectors and more sensitive to impacts in vertical sectors. This suggests why failures to detect prey occurred more often on the spiders' flanks. An alternative explanation for the greater sensitivity of *C. octotuberculata* to signals transmitted through vertical sectors relates to leg position. While the spider lays legs III on horizontal sectors, other legs (i.e. three times as many tactile sensors) are placed on vertical sectors. This hypothesis seems less plausible because it also predicts that *C. octotuberculata* would fail to detect prey more frequently in the north sector than in the south sector, since these spiders lay four legs (legs I and II) on the south sector but only two (legs IV) on the north sector. However, figure 2a and the average angular distribution of the failures to detect prey in the south sector indicate that this is not the case. Nevertheless, it is worth examining whether spiders such as *Argiope*, which pair the front and hind legs to form an X-shape, fail to detect prey more often in specific directions.

There are two possible reasons why radii running vertically were pulled more strongly by *C. octotuberculata*. One is that *C. octotuberculata* is not able to pull horizontally running radii as strongly as vertical radii. However, this is not supported by the observation of large inter- and intra-individual variability in pulling behaviour: in 31 cases among the 87 measurements, spiders actually pulled horizontally running radii more strongly. The second possible reason is that the spiders actively focus their attention on the web areas above or below their position on the hub of the web. Watanabe (1999) has revealed that hungry *O. sybotides* increases the tension of web threads by attaching a spiral silk stabilimentum to the web, and this enhances the sensitivity of the spider to small prey. In other words, satiated *O. sybotides* limits its attention to more profitable large prey. This is analogous to the results of this study, which indicate that *C. octotuberculata* may focus its attention on limited web areas rather than limited prey items. Attention focusing is considered to be adaptive behaviour since animals have finite information-processing capacity (Dukas 2004). The advantages of attention focusing may be more pronounced in small animals, such as spiders, with less cognitive ability than larger animals such as mammals or birds. Experiments that manipulate the rewards from particular web areas and observe the effect on thread-pulling behaviour would be a way to test this hypothesis.

Successful captures occurred more frequently in the web sector below the spider. This was not surprising because the lower half of their web is larger than the upper half, which is typical of spider vertical orb-webs. The lower half of the web is a more profitable foraging area because gravity helps the spiders to reach the trapped prey faster below the hub, and spiders generally position their heads downwards when waiting for prey (Masters & Moffat 1983; Zschokke & Nakata *in press*). Orb webs are typically vertically elliptic in most species (i.e. the vertical diameter is longer than the horizontal diameter; Blackledge & Gillespie 2002). The webs built by *C. octotuberculata* in this study were also vertically elliptic. Trapped prey struggling to escape sometimes tumble down the web (Zschokke *et al.* 2006). The

longer vertical diameter may retain tumbling prey for a longer period of time, and this may be a reason for building vertically elliptic orb webs. The elliptic shape may cause the spider to reduce the amount of attention given to its flanks, owing to the relatively low prey-interception frequencies in the relatively small horizontal sectors. Alternatively, a higher rate of prey-detection failures in horizontal sectors of the web might cause spiders to reduce the investment of silk in the horizontal sectors, resulting in vertically elliptic webs.

The results of this study suggest that attention focusing may have an important role in the foraging ecology of a sit-and-wait forager in nature. It implies that limitation of cognitive resources is a widely occurring phenomenon irrespective of foraging mode. The allocation of cognitive resources in the foraging ecology of animals has not been fully studied. Orb-web spiders are excellent study species for investigations in this area because the orb web is a sensory structure that extends beyond the spider's body and web modifications are relatively easy to observe.

I am very grateful to Dr Yusuke Shigemiyu for his help in collecting spiders and video recording. I am also grateful to two anonymous reviewers whose comments were helpful. This study was partly supported by a Grant-in-Aid from JSPS for Scientific Research (C) (20570025).

REFERENCES

- Barth, F. G. 2002 *A spider's world: senses and behavior*. Berlin, Germany: Springer-Verlag.
- Blackledge, T. A. & Gillespie, R. G. 2002 Estimation of capture areas of spider orb webs in relation to asymmetry. *J. Arachnol.* **30**, 70–77. (doi:10.1636/0161-8202(2002)030[0070:EOCAOS]2.0.CO;2)
- Díaz-Fleischer, F. 2005 Predatory behaviour and prey-capture decision-making by the web-weaving spider *Micrathena sagittata*. *Can. J. Zool.* **83**, 268–273. (doi:10.1139/z04-176)
- Dukas, R. 2002 Behavioral and ecological consequences of limited attention. *Phil. Trans. R. Soc. Lond. B* **357**, 1539–1547. (doi:10.1098/rstb.2002.1063)
- Dukas, R. 2004 Causes and consequences of limited attention. *Brain Behav. Evol.* **63**, 197–210. (doi:10.1159/000076781)
- Dukas, R. & Kamil, A. C. 2001 Limited attention: the constraint underlying search image. *Behav. Ecol.* **12**, 192–199. (doi:10.1093/beheco/12.2.192)
- Fauchald, P. & Tveraa, T. 2003 Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* **84**, 282–288. (doi:10.1890/0012-9658(2003)084[0282:UFPTIT]2.0.CO;2)
- Köhler, T. & Vollrath, F. 1995 Thread biomechanics in the two orb-weaving spiders *Araneus diadematus* (Araneae, Araneidae) and *Uloborus walckenaerius* (Araneae, Uloboridae). *J. Exp. Zool.* **271**, 1–17. (doi:10.1002/jez.1402710102)
- Landolf, M. A. & Barth, F. G. 1996 Vibrations in the orb web of the spider *Nephila clavipes*: cues for discrimination and orientation. *J. Comp. Physiol. A* **179**, 493–508. (doi:10.1007/BF00192316)
- Langley, C. M. 1996 Search images: selective attention to specific visual features of prey. *J. Exp. Psychol. Anim. Behav. Process.* **22**, 152–163. (doi:10.1037/0097-7403.22.2.152)
- Masters, W. M. & Markl, H. 1981 Vibration signal transmission in spider orb webs. *Science* **213**, 363–365. (doi:10.1126/science.213.4505.363)
- Masters, W. M. & Moffat, A. J. M. 1983 A functional explanation of top-bottom asymmetry in vertical orb webs. *Anim. Behav.* **31**, 1043–1046. (doi:10.1016/S0003-3472(83)80010-4)
- McLaughlin, R. L. 1989 Search modes of birds and lizards: evidence for alternative movement patterns. *Am. Nat.* **133**, 654–670. (doi:10.1086/284943)
- Schoener, T. W. 1971 Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* **2**, 369–404. (doi:10.1146/annurev.es.02.110171.002101)
- Watanabe, T. 1999 Web tuning of an orb-web spider, *Octonoba sybotides*, regulates prey-catching behaviour. *Proc. R. Soc. Lond. B* **267**, 565–569. (doi:10.1098/rspb.2000.1038)
- Wirth, E. & Barth, F. G. 1992 Forces in the spider orb web. *J. Comp. Physiol. A* **171**, 359–371. (doi:10.1007/BF00223966)
- Zar, J. H. 1998 *Biostatistical analysis*. Upper Saddle River, NJ: Prentice Hall.
- Zschokke, S. & Herberstein, M. E. 2005 Laboratory methods for maintaining and studying web-building spiders. *J. Arachnol.* **33**, 205–213. (doi:10.1636/CT04-72.1)
- Zschokke, S. & Nakata, K. In press. Spider orientation and hub position in orb-webs. *Naturwissenschaften*. (doi:10.1007/s00114-009-0609-7)
- Zschokke, S., Hénaut, Y., Benjamin, S. P. & García-Ballinas, J. A. 2006 Prey-capture strategies in sympatric web-building spiders. *Can. J. Zool.* **84**, 964–973. (doi:10.1139/Z06-074)